Different parts, different stories: climate sensitivity of growth is stronger in root collars versus stems in tundra shrubs

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Running head: Climate sensitivity among tundra shrub parts

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Abstract

Shrub densification has been widely reported across the circumpolar arctic and subarctic biomes in recent years. Long-term analyses based on dendrochronological techniques applied to shrubs have linked this phenomenon to climate change. However, the multi-stemmed structure of shrubs makes them difficult to sample and therefore leads to non-uniform sampling protocols among shrub ecologists, who will favor either root collars or stems to conduct dendrochronological analyses. Through a comparative study of the use of root collars and stems of *Betula glandulosa*, a common North American shrub species, we evaluated the relative sensitivity of each plant part to climate variables, and assessed if this sensitivity is consistent across three different types of environments in northwestern Québec, Canada (terrace, hilltop and snowbed). We found that root collars had greater sensitivity to climate than stems, and that these differences were maintained across the three types of environment. Growth at the root collar was best explained by spring precipitation and summer temperature, whereas stem growth showed weak and inconsistent responses to climate variables. Moreover, sensitivity to climate was not consistent among plant parts, as individuals having climate sensitive root collars did not tend to have climate sensitive stems. These differences in sensitivity of shrub parts to climate highlight the complexity of resource allocation in multi-stemmed plants. Whereas stem initiation and growth are driven by micro-environmental variables such as light availability and competition, root collars integrate the growth of all plant parts instead, rendering them less affected by mechanisms such as competition and more responsive to signals of global change. Although further investigations are required to determine the degree to which these findings are generalizable across the tundra biome, our results indicate that consistency and caution in the choice of plant parts are a key consideration for the success of future dendroclimatological studies on shrubs.

Introduction

Shrubs are one of the most responsive plant functional groups to recent climate change (Elmendorf *et al*., 2012) and their increase in abundance in tundra ecosystems have been cited as driver of the satellite-observed greening of the Arctic (Raynolds *et al*., 2006; Tape *et al*., 2006; McManus *et al*., 2012). The increase in shrub cover and abundance is widespread across northern circumpolar regions and has been recorded at both high latitude and high altitude sites in North America (Sturm *et al.,* 2001a; Tape *et al.,* 2006; Myers-Smith *et al.,* 2011a; Ropars & Boudreau, 2012), northern Europe (Bär *et al.,* 2008; Hallinger *et al.,* 2010) and Russia (Forbes *et al.,* 2010). Shrubs have either expanded in patch size (Sturm *et al.,* 2001a; Tape *et al.,* 2006; Ropars & Boudreau, 2012; Tremblay *et al*., 2012), recruited in areas where they were less abundant in the past (Sturm *et al.,* 2001a; Frost *et al.,* 2013; Frost & Epstein, 2014; Buntgen *et al*., 2015) or have increased in height (Myers-Smith *et al*., 2011b; Paradis *et al*., 2016). Though this increase in tundra shrubs has been attributed to recent warming in tundra ecosystems (Elmendorf *et al*., 2012; Ropars *et al*., 2015), the climate sensitivity of shrub growth has been demonstrated to be variable across the tundra biome (Myers-Smith *et al*., 2015a).

Understanding how shrub growth is controlled by climate is key to predicting vegetation change and its associated impacts on ecosystem function in a warming tundra biome. In treeless ecosystems, erect shrubs provide structure for both plant and animal communities (Tape *et al*., 2016) and modify important ecological processes and physical characteristics of the environment (Cushman *et al.,* 2010). In tundra regions, shrubs are expected to have complex and sometimes seasonally contrasting or species-specific effects on permafrost dynamics or soil temperature regime (Sturm *et al*., 2001b; Blok *et al*., 2011; Myers-Smith & Hik, 2013; Paradis *et al*., 2016) and absorption of solar radiation (Chapin *et al*., 2005; Williamson *et al*., 2016). Shrubs provide important habitat and food sources for moose, caribou, ptarmigan, hare and other wildlife species

74 (Tape *et al*., 2010, 2016; Boelman *et al*., 2015; Christie *et al*., 2015), but might also reduce lichen
75 availability in caribou winter ranges (Joly *et al*., 2007). Since erect shrub species have a
76 significant impact on the dynamics and physical properties of arctic and subarctic ecosystems, it
77 is essential to better understand the factors driving their growth and rapid expansion.
78 Dendrochronological approaches have successfully been applied to shrub species to analyze
79 temporal and spatial processes in fast-changing tundra ecosystems (e.g. Bär *et al*., 2008; Forbes
80 *et al*., 2010; Blok *et al*., 2011; Myers-Smith *et al*., 2015a; Ropars *et al*., 2015). Like trees, shrubs
81 form annual growth rings that can be related to climate variables (e.g., Myers-Smith *et al*., 2015a)
82 or disturbances in ecosystem processes such as landslides (e.g., Gers *et al*., 2001) and permafrost
83 degradation (e.g., Gaertner-Roer *et al*., 2013). However, the multi-stemmed growth form of
84 shrubs has several ecological and physiological implications that may influence climate
85 sensitivity among their different parts. For example, shrubs have the potential to allocate
86 resources to different stems and roots depending on environmental conditions (Pajunen, 2009)
87 and competition for light and nutrients in dense shrub patches could lead to differential stem
88 growth within an individual (Hallinger *et al*., 2010; Myers-Smith *et al*., 2015b). Moreover, there
89 is still very little known about how stems are initiated and replaced within a shrub individual (but
90 see Charles-Dominique, 2011). All of these complex interactions could result in different radial
91 growth patterns between the stems of a single individual. Despite these considerations, stems and
92 root collars (i.e. the oldest part of a shrub, found at the junction between roots and stems) are
93 often used without distinction both across (Myers-Smith *et al*., 2011a) and within studies
94 (Dumais *et al*., 2014).
95 A review of shrub dendrochronological studies reveals that stems are more frequently used
96 than root collars (44/69 studies compared to 15/69; Fig. 1 and Table S1). The strong preference
97 towards stems likely arises from some of the following reasons: root collars are hard to access in

certain environments and in areas of continuous shrub cover, their sampling is destructive and their identification can be difficult, especially when shrub individuals display complex morphologies such as adventitious roots and buried stems (Myers-Smith *et al*., 2015b). As a consequence, it is often easier to sample the largest and/or longest stems of an individual, even if it does not track the entire shrub growth record (De Witte *et al*., 2012). However, comparing the climate sensitivity of shrubs across different sites or regions could be potentially problematic if different shrub parts exhibit different growth trends that are influenced not only by climate but also by within-individual competition and resource allocation.

The growing number of studies dealing with the sensitivity of shrub growth to climate change highlights the need to converge towards standardized methods in dendroecology applied to shrubs, especially in the fast-changing tundra biome. Here, we present a comparative study of the use of root collars and stems in dendroclimatology analyses. Specifically, we aim (1) to evaluate the relative sensitivity of stems and root collars to climate, and (2) to evaluate if this relative sensitivity is consistent across different types of environments. We hypothesize that climate sensitivity will be higher for root collars, given that they integrate growth from the whole individual, and that this difference will be maintained across the landscape.

Materials and methods

Study area and climatic trends

The study area is located around the Boniface River research station (Centre d'études nordiques, http://www.cen.ulaval.ca/page.aspx?lien=stationboniface; 57° 45′ N, 76° 20′ W), about 10 km south of the Arctic treeline in subarctic Québec (Canada). The area lies within the discontinuous permafrost zone (Payette, 2001) and belongs to the shrub subzone of the forest-tundra ecotone (Payette, 1983). At the landscape scale, shrub tundra covers *ca.* 70% of the well-drained sites (Payette *et al.*, 2008). Wetlands, which include palsas and snowbeds, cover 7% of the terrestrial area. *Betula glandulosa* Michx. (hereafter referred to as dwarf birch), a multi-stemmed species widely distributed in North America, is the most abundant shrub species and is responsible for most of the shrub expansion observed in the study area (Ropars & Boudreau, 2012). According to Ju & Masek (2016), this is the Canadian region where the greening was the most extensive in the last three decades. Large herbivores (caribou: *Rangifer tarandus* L.) are present in the area, but browsing is mostly restricted to *Salix* species.

The closest meteorological station (Inukjuak Meteorological Station, Environment Canada; 58º 28' N, 78º 05' W; 130 km northwest of the study site) recorded an annual mean temperature of -7 ºC for the 1971-2000 period, with the highest and lowest mean monthly temperatures recorded in July (9.4º C) and February (-25.8 ºC), respectively (Canadian climate normal; Environment Canada, 2016). Annual precipitation averaged 460 mm, of which 42% fell as snow (Canadian climate normal; Environment Canada, 2016). Between 2000 and 2009, mean annual temperature has reached - 5.5 ºC, with July and February temperatures averaging 11.7 ºC and - 24.8 ºC. Like many regions in northern Québec, Inukjuak is experiencing a warming trend that began in the early 1990s (Chouinard *et al.*, 2007; Bhiry *et al*., 2011).

Site selection and field sampling

The root collar and the two main stems of dwarf birch were sampled in three different environments to assess potential site-driven differences in climate sensitivity: sandy terraces (hereafter referred to as terraces), low-altitude hilltops (hereafter referred to as hilltops) and snowbeds. The terraces are well-drained, low-altitude sites located on the banks of the Boniface River. They are characterized by lichens, graminoids and large patches of shrub species, mainly dwarf birch, although willows and alders can be found close to the river. The hilltops are characterized by the presence of arctic-alpine species and exposed mineral soil. Snowbeds are periglacial environments where snow accumulates preferentially during winter and melts later in the growing season, sometimes as late as mid-July. Consequently, they are characterized by plant species well-adapted to winter conditions and to an excess of moisture in the first half of the growing season (Payette & Lajeunesse, 1980; Filion & Payette, 1982; Morin & Payette, 1986). One site in each environment type was randomly selected from a pool of 147 identified sites (50 terraces, 50 hilltops, and 47 snowbeds; see Ropars *et al.*, 2015 for more details on site selection).

In summer 2010, we selected and uprooted 20 dwarf birch individuals at each site. We prioritized large and relatively isolated individuals with a circular form, as they were thought to be older individuals grown from seed. When such individuals were not available, particular attention was taken to discard individuals for which the root collar could not be easily identified. Dwarf birch individuals grown from seeds usually display a short (< 3cm) but well-defined root collar, located between the root and stem systems (Fig. 1c). From the three to six main stems directly emerging just above the root collar, we selected the two largest ones and cut them as close as possible to the root collar and the soil surface. The two stem samples and the root collar

of each dwarf birch individual were collected, carefully cleaned, and left to fully dry at room temperature.

Radial growth measurement

Dwarf birch root collars were sliced (*ca*. 25 μm) using a rotary microtome after being boiled for at least 3 hours. Thin sections were then stained with safranin (1% solution, Safranin O, Fischer Science Education), dried and permanently mounted with a 66% toluene solution (SHUR/mount^{TM} liquid cover glass, Triangle biomedical sciences). Digital photographs of each sample were taken using a binocular-mounted camera (Olympus SZ61 with a SC100 camera). Root collars were discarded if they could not be sliced perpendicularly (stems and roots were too intermingled), or if they were rotten. Of the 60 root collars processed for the three sites, 46 were kept for further analyses (terrace: 15, hilltop: 16, snowbed: 15). The two largest stems of each of these 46 individuals (92 stems) were processed following the above procedures.

Using digital photographs, we aged each root collar and stem sample with the ImageJ freeware (v. 1.40g) while ring widths were measured using the dendrochronological software LignoVision (v. 1.36, Rinntech). If possible, ring widths were measured along two opposite radii and averaged for each sample. Growth measurements were visually examined and statistically verified with COFECHA, a widely used statistical crossdating program (Holmes, 1983). We used the mean detrending method for every root collar and stem ring-width series to allow comparison between individuals. Incomplete rings were frequently encountered, but easily detectable. Unlike other willow and birch species growing at their altitudinal limit (Wilmking *et al*., 2012), no missing rings were identified in the root collar samples.

Measuring climate sensitivity

The climate sensitivity of root collars and stems was measured using mixed-effects models. We used ring-width data for the period 1947-2009, for which monthly temperature and precipitation data were available from the Inukjuak Meterological Station. We ran a series of linear mixed-effects models using standardised (mean centered) ring width as a response variable, monthly temperature and/or precipitation variables (singly or in combination; see Table S2 for the full list of models) and the sample type (root collar vs stem) as interacting predictors, and with year as a random effect. We also ran a null model, i.e. a model with the same random effect structure that does not include any climate variables as fixed effects to serve as baseline for the climate sensitivity analysis (Ettinger *et al*., 2011; Myers-Smith *et al*., 2015a). We allowed for interactions between fixed effects because we were specifically interested in the potentially different climate responses of shrub root collars and stems. We ran a separate series of models for each site, as the added complexity of including a site level in the model structure while allowing for random slopes caused convergence issues. We ran the analyses with the lme4 package (R version 3.2.2), using the maximum likelihood estimation for model selection and the restricted maximum likelihood estimation to estimate slopes.

As our interaction models (sample type * climate) were driven mostly by the stronger response of the root collars, we also ran separate models for stems vs root collars at each site to check whether stems might be more responsive to a different climate variable. We additionally ran the same model structure with the nlme package to compare model results to models with a temporal autocorrelation structure, and using raw (non-standardized) ring-width data and a subset of the data restricted to the common period covered by both stem and root collar chronologies (1960-2009). These complementary analyses yielded the same results, and thus are not presented

in the main text (see Table S3 for results obtained with raw data, the 1960-2009 subset and using the nlme package).

We used model selection analysis to identify the best climate model(s), i.e. the variables that best explain variations in radial growth. We ranked the models according to the Akaike information criterion (AIC) and calculated the difference between each model and the null model, which we denoted by ΔAIC_{null}. ΔAIC_{null} is used as a measure of the sensitivity of radial growth to specific climate variables (Myers-Smith *et al*., 2015a). As the AIC only assesses the relative quality of competing models, but not the absolute goodness of fit, we also calculated the marginal and conditional R^2 of each model with the r.squaredGLMM function of the MuMin package (R version 3.2.2). The conditional R^2 represents the amount of variance explained by all the fixed and random effects in the model, while the marginal R^2 is the amount of variance explained by the fixed effects only (Nakagawa & Schielzeth, 2012).

Linear models

To investigate whether stem and root collar sensitivity were correlated or decoupled within an individual, we ran a linear model with ring width as a function of the two best climate variables (July temperature and March precipitation) identified through the model selection described above for each individual. We then compared whether the slopes differed between plant parts for each individual. We also used these slope values to test whether there is a significant relationship between climate sensitivity of root collars and their stem counterparts. To do so, we ran a linear model with the slope values obtained for stems as a function of the ones obtained for root collars. We applied a squared-root transformation to the slope values to attain normality (Legendre & Legendre, 1998). A constant was added to the slope values prior to transformation to cope with negative numbers.

Results

Sensitivity of stems and root collars to climate

We found greater sensitivity of *Betula glandulosa* root collars versus stems across our sampling sites (Fig. 2). Climate sensitivity of stems was generally weak, the null model ranking between the 4th and 7th best model (Table S1). Moreover, the proportion of the variance in growth explained by climate variables (i.e. marginal R^2) for root collars was at least twice as high as for stems in the snowbed and hilltop sites, and there was a similar but weaker trend for the terrace site.

Climate variables best explaining growth

We found that March precipitation and July temperature best explained shrub growth, but with a strong interaction with sample type. Root collars showed a consistent positive response to these two climate variables, but not stems (Fig. 2). Moreover, when stems and root collars were analyzed separately, the latter showed greater climate sensitivity than stems to most climate variables (monthly mean temperature and total precipitation; Fig. 3). The difference in AIC score between the null model and the best climate model was systematically higher for root collars than for stems in each type of environment (Table 1). March precipitation and July temperature best explained the growth at the root collar, and this relationship was maintained across the landscape. On the other hand, stems showed weak and inconsistent responses among the three environments; August, May and April temperature best explained stem growth in snowbed, hilltop and terrace, respectively.

Climate sensitivity of individuals among shrub parts

Individual-level climate sensitivity did not show a consistent trend among root collar and stems (Fig. 4). Individuals having a climate sensitive root collar did not tend to have climate sensitive stems, as only five climate sensitive root collars out of 42 had one or two of their stem counterparts sensitive to climate as well. Of the 11 climate sensitive stems, seven were associated with climate sensitive root collars. Moreover, root collar and stems from the same individual showed opposite significant relation with July temperature in one particular case (individual S27, Fig. 4). The climate sensitivity of stems to both July temperature (linear model, $F_{1,90} = 2.927$, $P = 0.091$) and March precipitation (linear model, $F_{1,88} = 1.624$, $P = 0.206$) was not explained by the climate sensitivity of their root collar counterparts.

Root collar and stem samples characteristics

We found that root collar ages were greater than stem ages and that ages varied across the different environments sampled. Root collar samples averaged 41 years of age, but ranged between 10 and 96 (Table 2). The oldest root collar was from an individual growing on a hilltop, whereas the youngest were found in the snowbed environment. There was no difference in root collar samples age between the three types of environment ($F_{1,3} = 1.02$, $P = 0.369$). Stem samples averaged 23 years of age, but some reached over 60 years in the hilltop environment. The stems of dwarf birch individuals growing in the snowbed site were younger (18 years old compared to 27 and 25 for hilltop and terrace; Tukey multiple comparison, $P < 0.01$) and longer (from the root collar to the tip of the stem) than those of individuals growing on the hilltop and terrace sites (Table 2; 133 cm compared to 92 cm and 102 cm for hilltop and terrace, Tukey multiple comparison, $P < 0.01$).

Discussion

In this study, we demonstrated that different parts of an important tundra shrub species in North America, *Betula glandulosa*, have contrasting responses to climate, with root collars exhibiting far greater sensitivity than stems. Growth at the root collar was best explained by spring precipitation and summer temperature, and this relationship was maintained across the landscape. Stems, on the other hand, showed weak and inconsistent responses. These results highlight the complexity of resource allocation in multi-stemmed shrubs and call for caution in sampling when aiming to assess the climate sensitivity of shrub growth.

What explains the difference in sensitivity of root collars vs stems?

The multi-stemmed structure of shrubs results in complex resource allocation patterns among plant parts that could dampen the influence of climate on stems growth. In their review of intra-plant competition, Sadras & Denison (2009) concluded that plant individuals might use competition-like mechanisms to allocate resources such as nutrients, but only if it increases overall individual fitness. Competition within plant individuals is known to lead to trade-offs between size and number of plant units (Sadras, 1995; Chikov, 2008; Sadras & Denison, 2009) as well as between vegetative and reproductive structures (e.g. Liu *et al*., 2007; Quilot & Genard, 2008). The vertical growth of shrubs can also be limited by the abrasive effect of windblown ice particles (Sonesson & Callaghan, 1991), resulting in differential growth patterns among stems. Moreover, the drivers of stem initiation at the root collar are poorly understood. Light availability promotes stem initiation of *Rhamnus cathartica* L., a deciduous shrub growing in southern Québec (Charles-Dominique *et al*., 2012) and an increased herbivory pressure is known to alter the vertical structure of *Salix* and *Betula* species in northern Alaska (Tape *et al*. 2010; Christie *et al*., 2014). The growth of each stem is therefore affected not only by climatic and other

environmental conditions, but also by differential resources allocation among plant parts that enhances the individual's global fitness. On the other hand, root collars integrate the growth of each plant part. Thus, they might be less affected by competition-like mechanisms and more responsive to climate.

Root collars showed consistent responses to climate variables across the landscape, with both July temperature and March precipitation promoting enhanced radial growth. Warmer temperatures during the short growing season have been identified as key factors for promoting shrub growth in different Arctic regions (e.g. Bär *et al*., 2008; Forbes *et al*., 2010; Hallinger *et al*., 2010; Myers-Smith *et al.* 2015a). Higher precipitation in March could reduce the risk of frost damage following early leaf-out, and protect buds and stems from the abrasive effect of drifting ice particles (Sonesson & Callaghan, 1991). Among other possible explanations, an increase in snow precipitation could also promote a better radial growth by increasing water discharge and thus water availability in early summer. Greater snow accumulation may also lead to greater insulation, higher soil temperature and increased microbial activity, which in turn could lead to higher nutrient availability (Chapin *et al*., 2005).

To our knowledge, the present study is the first to compare climate sensitivity among different parts of shrub individuals. The harsh climatic conditions of arctic and alpine regions can result in intra-plant growth irregularities that could influence climate sensitivity, such as missing or incomplete rings (Hallinger *et al*., 2010; Buchwal *et al*., 2013). The distribution of these growth irregularities has been shown to be heterogeneous among shrub parts (Hallinger *et al*., 2010). For *Salix polaris* Wahlenb for instance, the growth at the root collar and in the belowground system was consistently greater than the growth in stems (Buchwal *et al*., 2013). While serial sectioning (Kolishchuk, 1990), a technique consisting in repeated tree-ring width measurements along shrub stems, allows to properly date woody plant individuals (Hallinger *et*

326 *al*., 2010; Wilmking *et al*., 2012; Buchwal *et al*., 2013; Hollesen *et al*., 2015), it also emphasizes
327 growth heterogeneity among plant parts. For different northern pine and spruce species,
328 differences in growth-climate relationships have been observed among plant parts, breast-height
329 and upper stem samples being more sensitive to previous and current season temperatures and
330 moisture, respectively (Kozlowski *et al*., 1991; Chhin & Wang, 2008; Chhin *et al*., 2008, 2010).
331 Our findings suggest that complex controls are also at play in determining the growth of shorter-
332 statured but multi-stemmed plants.
333
334 *Implication of the study*
335 Changes in shrub cover will play an important ecological role in arctic regions, emphasizing the
336 need to better understand their drivers and to predict their magnitude. Large scale meta-analyses
337 focusing on many taxa are useful to address these questions (see Myers-Smith *et al*., 2015a), but
338 their conclusions could be challenged by a lack of consistency in sampling methods across
339 studies. Our results show that root collars are consistently more climate sensitive than stems for a
340 widely distributed shrub species, *B. glandulosa*, one of the most commonly reported shrub
341 species to be expanding in tundra ecosystems (Tape *et al*., 2006; Myers-Smith *et al*., 2011a;
342 Ropars & Boudreau, 2012; Tremblay *et al*., 2012). Moreover, a climate sensitive root collar was
343 not necessarily associated with climate sensitive stems (Fig. 4). In their recent meta-analysis,
344 Myers-Smith and collaborators (2015a) found greater climate sensitivity in northwest Russia
345 compared to North America. Based on our literature review (Fig. 1 and Table S1), these
346 differences could be partly explained by the differential use of stems and root collars across
347 studies. Indeed, most Russian studies have used root collars (8 out of 11 studies, 73%), whereas
348 only a third of North American ones did (10 out of 30 studies, 33%; Table S1). The sensitivity of
349 North American shrubs could therefore have been underestimated and could overlook the

potential increase in shrub abundance and canopy height. While the differences among shrub parts have been overlooked in the past, our study highlights the importance of establishing consistent sampling protocols for shrub dendrochronological analysis.

How do we move forward with future dendroecological analyses?

While this study clearly demonstrates that different plant parts show different climate sensitivity, further investigations are required to understand how generalizable our findings are across the tundra biome. In our study, we focused on one shrub species, *Betula glandulosa*, growing in a specific subarctic area of North America. Shrub species having similar growth forms and branching architecture (like alders and willows) could potentially also show similar differences in climate sensitivity among plant parts, but a multispecies comparison would be needed to confirm this hypothesis. Architectural studies of shrubs are arising in the scientific literature and could bring us a step further in our comprehension of energy allocation among plant parts (Charles-Dominique, 2011). We therefore propose that architectural and comparative dendrochronological studies be combined to account for potential differences in growth patterns among shrub parts. If dissimilarities between plant parts are also observed in other sites and species, we urge for the establishment of a standardized sampling methodology for future studies. Based on the fact that root collars were more climate sensitive than stems, we propose that future studies systematically sample shrub individuals as close as possible to the root collar.

Understanding the dynamic of shrub populations and the drivers of their growth is key to assess and predict global ecosystem processes under climate change, especially in Arctic regions where they structure plant communities. Our study clearly demonstrates that root collars provide a better integration of the climate sensitivity of shrub individuals for a widely distributed species

374 in North America, *Betula glandulosa*. Root collars were more climate sensitive than stems and
375 showed consistent sensitivity to July temperature and March precipitation across three different
376 types of environments in the Boniface River region. Finally, we found no consistency between
377 shrub parts, individuals having a climate sensitive root collar not necessarily having climate
378 sensitive stems. While different shrub parts have been sampled for dendrochronological analyses
379 in the past, this study urges for a standardized sampling methods. To reveal reliable climate
380 sensitivity of tundra shrub species and, more importantly, to conduct multi-sites and multi-
381 species analysis, we propose to systematically sample at root collar.
382

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Tables

Table 1 Results from the model selection using Akaike information criterion. The sensitivity (i.e. difference between the best and the null model, in terms of ΔAIC), the marginal R^2 (i.e. the amount of variance explained by fixed effects) and the conditional R^2 (i.e. the amount of variance explained by both fixed and random effects) are shown only for the more plausible model(s) for stem and collar in each type of environment. T and P stands for temperature and precipitation, respectively.

Site	Shrub part	Best climate model	Sensitivity (ΔAIC_{null})	Marginal R^2	Conditional R^2
Snowbed	Root collar	July T + March P	19.0	0.29	0.53
	Stem	August T	7.1	0.15	0.31
Hilltop	Root collar	July T + March P	16.2	0.13	0.24
	Stem	May T	2.2	0.02	0.09
Terrace	Root collar	July and August T	12.2	0.07	0.13
		July T + March P	11.8	0.06	0.12
	Stem	April T	3.8	0.04	0.15

Table 2 Information on individual root collar and stem samples in three different types of environments in the Boniface River region, Nunavik, Québec, Canada. The stem length refers to the measure (in cm) from the root collar to the tip of the stem. The numbers in brackets (second column) represent the sample size.

		Age		Length	
		Mean value (years)	**SD**	**Mean value (cm)**	**SD**
Root collar	Snowbed (15)	35.3	17.5	-	-
	Hilltop (16)	45.2	20.7	-	-
	Terrace (15)	43.5	21.1	-	-
	Mean value	41.4	20.5	-	-
Stem	Snowbed (30)	17.9	9.5	146.8	31.1
	Hilltop (32)	26.9	14.5	92.4	16.4
	Terrace (30)	25.3	12.2	101.8	21.3
	Mean value	23.4	13.0	109.1	28.9

Figure captions

Figure 1 (**a**) Map of shrub sampling methods for dendroclimatological analyses in northern hemisphere. The black star represents our study area near the Boniface River research station, Nunavik, Québec, Canada; darker dots represent regions for which more than one study took place. (**b**) General landscape around the Boniface River research station, with extensive *Betula glandulosa* thickets. (**c**) An uprooted *B. glandulosa* individual with large proportion of its stems and roots removed. The location of the root collar, roots and stems are shown.

Figure 2 Differences in climate sensitivity of growth for March precipitation (**a** – **c**) and July temperature (**d** – **f**), the two best climate models, between stems (red) and collars (blue). Solid lines and shaded areas indicate the slope estimates and 95% confidence interval for the mixed model analyses.

Figure 3 Sensitivity of collar and stem growth to monthly (**a**) precipitation and (**b**) temperature, as expressed by the difference between the AIC of each linear models and the AIC of the null model. The metric "sensitivity" was obtained by multiplying the ΔAIC_{null} by +1 or -1 depending on the sign of the slope of the regression to represent positive and negative growth responses, respectively. “P” preceding a month stands for previous year.

Figure 4 The linear model results in climate sensitivity for each individual chronology, for both stems (red) and root collars (blue). Climate sensitivity to July temperature (**a**, **c**, **e**) and March precipitation (b, d, f) are shown for individuals growing on snowbed (**a**, **b**), hilltop (**c**, **d**) and

terrace (**e**, **f**). Bars are the slope and standard error (linear models). Filled bars indicate regression slopes that are significantly different from 0 ($p < 0.05$).